THE CAMBIUM AND ITS DERIVATIVE TISSUES

NO. IX. STRUCTURAL VARIABILITY IN THE REDWOOD, SEQUOIA SEMPERVIRENS, AND ITS SIGNIFICANCE IN THE IDENTIFICATION OF FOSSIL WOODS

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INTRODUCTION

Systems of classifying the woods of conifers and dicotyledons have developed largely through trial and error, and in many cases do not provide a reliable basis for the identification of fossilized specimens. This is due to the fact that comparatively little is known concerning the limits of variability of the diagnostic criteria used in the construction of keys.

In the seventh paper of this series (Bailey, 3) it was shown that a number of the so-called transitional Mesozoic Coniferæ fall within the range of variability of living representatives of the Pinaceæ-Abietoideæ. If *Protocedroxylon, Planoxylon, Protopiceoxylon,* etc., are to be classified as Protopinaceæ or Araucariopityeæ, then so should certain specimens of the wood of *Cedrus, Keteleeria,* and other extant genera. Such paradoxical situations can not be fully clarified until large collections of authentic specimens are assembled, not only from different genera, species, and geographical races, but also from different parts of the tree and from trees growing under different environmental conditions.

In choosing a species for an investigation of the range of variability of anatomical characters, it seemed advisable to select the redwood, *Sequoia sempervirens* Endl. This tree is of unusual interest not only because of its large size and longevity, but also because it belongs to a genus which has been, and still is, the subject of frequent discussion in paleobotanical literature.

MATERIAL

Most of the material from mature stems of large diameter was collected by Professor A. E. Douglass in connection with his investigation of tree rings. Entire cross sections were secured from different heights in the tree and from trees growing in different parts of the extensive range of the redwood. Small specimens suitable for anatomical study were removed along specific radii of these huge cross sections. Specimens from roots, branches, and stems, of both seedling-

trees and sprout-trees, were collected by the senior author in Mendocino and Monterey counties. Additional material was obtained through the kind assistance of Mr. Frank Poulter, Professor Emanuel Fritz of the University of California, Mr. H. L. Person of the California Forest Experiment Station, Dr. D. T. MacDougal and Mr. F. W. Haasis of the Carnegie Institution, and others.

GROWTH LAYERS

The growth layers of the redwood, as seen in transverse sections, vary considerably in width, in the ratio of latewood to earlywood, and in the abruptness of the transitions between thin-walled and thick-walled tracheids, *Figs. 1-13*. In young trees growing under favorable environmental conditions, the growth layers of the stem commonly attain a width of from 4-10 millimeters, *Fig. 11*. During the subsequent development of the trees, the rings tend to become narrower and narrower, *Figs. 3-5*, and may actually be reduced at times to the theoretical minimum of two tracheids, i.e., one thin-walled cell and one thick-walled cell, (a) in *Fig. 5*. Such sequences of growth layers of decreasing width, although of not infrequent occurrence, are by no means a characteristic feature of all redwoods. The species grows naturally in forests of the "selection type," and a large proportion of the trees originate as sprouts which develop in deep shade and are forced to grow for a varying period of years in a more or less suppressed condition. Thus, many of the trees in virgin forests have relatively narrow rings throughout the stem, or alternating zones of narrow and wide rings; for even old suppressed trees may form wide rings, *Fig. 13*, when released from the competition of their dominating neighbors (Fritz, 12), or in response to specific tropisms, *Fig. 6*. Excentric arcs of abnormally wide growth layers, false rings, *Fig. 12*, incomplete rings (Fritz and Averell, 11), and burly or curly structures are of very common occurrence. As stated by Fisher (10), "the tree's vitality is so great, it endures so many vicissitudes, and suffers from so many accidents in the centuries of its existence, that the grain of its wood becomes uneven in proportion as its life has been eventful." The growth layers of branches and roots, *Figs. 7-10*, tend to be narrower than those of stems of comparable ages. It is evident, accordingly, that in the redwood as in many other Coniferæ, width of annual ring is a fluctuating character which varies within rather wide limits, not only within different parts of a single tree, but also within homologous portions of trees having different developmental histories.

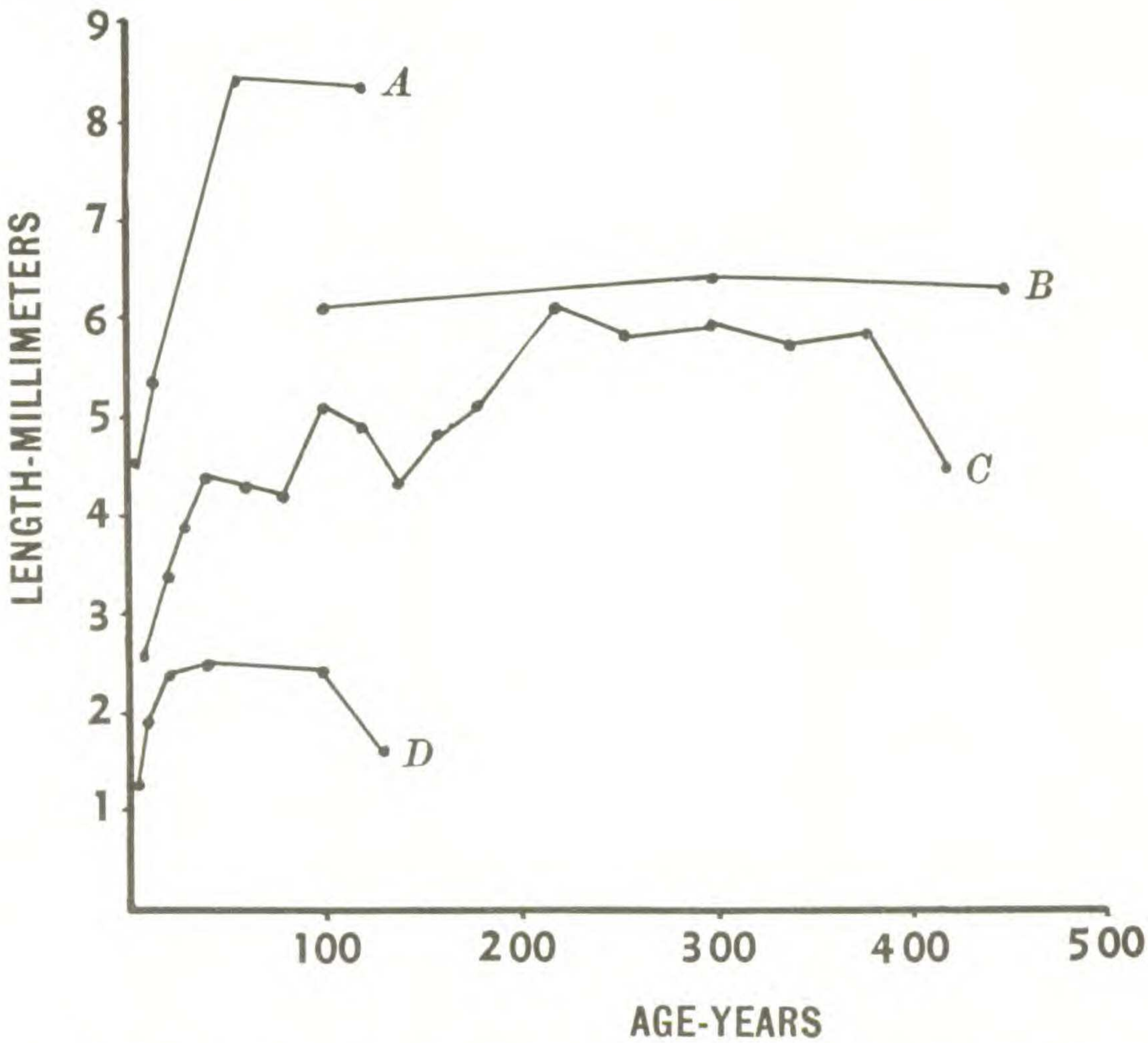
In narrow rings from the peripheral portions of old stems, roots, and branches, *Figs. 4, 5, 8,* and *10*, the ratio of latewood to earlywood is

low, 1:6 to 1:20, and the transitions between thin-walled and thick-walled tracheids are very abrupt; whereas in wide rings, *Figs. 3, 6,* and *13,* the ratio tends to be higher, 1:3 to 4:7, and the transitions may be either gradual, *Fig. 13,* or abrupt, *Figs. 3* and *6.* In the inner rings of stems and branches, the ratio of latewood to earlywood tends to be lower in the wider rings, *Figs. 1, 2, 7, 11,* and *12,* and the transitions between the two types of tracheids to be so gradual that it is difficult to determine with certainty just where the earlywood leaves off and the latewood begins. Paul (23) and Luxford and Markwardt (22) have shown that in the case of second-growth redwood, specific gravity and strength values are lower in open grown trees with large crowns and wide rings than in trees of densely stocked stands with small crowns and narrower rings, the differences being due, in ultimate analysis, to variations in the ratio of latewood to earlywood. It should be emphasized, however, that there are numerous exceptions to these general tendencies, particularly in "compression wood" (Hartig, 16), and in tissues growing under abnormal conditions. For example, *Fig. 9* is a transverse section of "compression wood" from the under side of an old slowly growing branch. The narrow rings are composed entirely of thick-walled tracheids, and it is difficult to distinguish the limits of the individual growth layers.

TRACHEARY ELEMENTS

The size, form, and arrangement of the tracheids—of both earlywood and latewood—vary markedly in different parts of a single tree and in homologous parts of trees which have had different developmental histories. As shown by Sanio (27), Hartig (15), Shepard and Bailey (29), and subsequently by many others, the tracheids of Coniferæ are smaller in the inner than in the outer rings of the stem. This is due primarily to an increase in the length and tangential diameter of the cambial initials, particularly during the earlier years of the meristematic activity of the cambium (Hartig, 15; Bailey 1, 2). Thus, in passing from the pith outward through the xylem of old, straight-grained, symmetrical stems, the derivatives of the cambium become longer and wider until they eventually attain dimensions which remain more or less constant through succeding annual rings. The detailed investigations of Bailey and Tupper (4) indicate that in any particular radius of the stem, the size-on-age curve, or one or more portions of it, may deviate from the normal, owing to the effects of various modifying factors. For example, the distorted tissue formed subsequent to injury, or in response to abnormal conditions of growth, commonly possesses shorter tracheids than normal tissue. Similarly, tissue formed in regions of the tree

where there are mechanical stresses, i.e., at the junction of stems and roots or branches, or in bent or deformed stems, tends to have smaller tracheids than normal, straight-grained tissue. Therefore, the largest tracheids usually occur in the "clear length" of tall trees or that central portion between the swollen base and the crown which is devoid of branches; whereas smaller tracheids are characteristic of suppressed branches and of the physiologically dwarfed stems of depauperate plants.



TEXT FIGURE 1. Graphs illustrating variations in length of tracheary elements in passing from the innermost to the outermost secondary xylem. (A) Root: 2½ inches in diameter and 120 years old. (B) Root: 12 inches in diameter and 450 years old. (C) Stem: 5 feet in diameter and 420 years old, at stump height. (D) Branch: 1¾ inches in diameter and 130 years old, from the crown of a huge old tree. Each point on the graphs represents an average of 100 measurements.

As indicated in *Text fig. 1*, the tracheary elements of the redwood fluctuate in length much as they do in other representatives of the Coniferæ, but the range of variability tends to be greater than in smaller

and shorter-lived species. In the material examined by us, the tracheids vary from less than a millimeter to more than a centimeter in length. The longest cells occur in roots, *Text fig. 1, A* and *B*, and the clear length of tall stems, whereas shorter cells are formed in branches, *Text fig. 1, D*, and in suppressed stems.

The tracheids of *Sequoia sempervirens* fluctuate from less than 10 μ to more than 100 μ in diameter. In radial strips from the clear lengths of huge mature trees, the average tangential diameter of the tracheids commonly varies from approximately 20 μ in the innermost rings to 60 μ in the outer growth layers, *Figs. 1, 4,* and *5*. In old suppressed branches, on the contrary, the differences in diameter, 18 to 24 μ, may be scarcely detectable, *Figs. 7-9*. In the roots of the Abietineæ, the widest tracheids frequently occur in close proximity to the primary elements; whereas in the redwood the tracheary cells commonly are smaller in the innermost rings, *Figs. 15* and *16*, but rapidly attain dimensions which are comparable with those of the tracheids of the outermost rings of old stems (compare *Figs. 3-5*, and *10*).

The form of the tracheids, as seen in transverse sections, varies from square or rectangular, *Figs. 2* and *5*, to asymmetrically pentagonal or hexagonal, *Figs. 4, 10,* and *16*, and in typical "compression wood" to oval or nearly circular, *Figs. 6* and *47*. Radially narrow rectangular forms are characteristic of the outermost tracheids of wide rings and of the entire latewood of such growth layers as those illustrated in *Figs. 4, 5, 8,* and *10*. Radially elongated forms are of common occurrence in large-celled earlywood of old stems and roots, *Figs. 4, 6, 10,* and *16*. Owing to variations in the size of tracheids and in the thickness of their walls, specific gravity is not a constant for either earlywood or latewood.

INTER-TRACHEARY PITTING

The more conspicuous variations in the size, form, number, and orientation of the bordered pits in the radial walls of the tracheids, *Figs. 20-30*, are more or less closely correlated with fluctuations in the size of these cells and in the thickness of their walls. In other words, the bordered pits tend to become larger and more numerous as the tracheids increase in radial diameter in an expanding stem or root (compare *Figs. 20* and *25, 26* and *30, 28* and *29*); but, within each growth layer, they decrease in size and number in passing from the larger thin-walled elements of the earlywood to the smaller thick-walled cells of the latewood. The pits commonly tend to be more numerous toward the overlapping ends of the tracheids and in those portions of the radial walls which are in contact with the terminal portions of

adjoining tracheids. Furthermore, the pits tend to be more numerous in relatively narrow rings than in unusually wide growth layers. Therefore, in studying variations in tracheary pitting, it is essential not only to compare homologous parts of the growth layers, but also equivalent areas of the walls of the tracheids.

The radially narrow tracheids of the latewood and the earlywood tracheids of the inner growth layers of stems and branches usually have a single row of small bordered pits; i.e., a single bordered pit is formed over each of the more or less conspicuous primary pit-fields, *Fig. 25*. On the contrary, the large earlywood tracheids of old stems and roots may form from 1-4 large bordered pits over each of the transversely elongated primary pit-fields, *Figs. 20-23*. Where the pits are approximated vertically, *Fig. 20*, the crassulæ[1] ("Bars of Sanio") are rodlike, and the primary walls have a scalariform appearance; where they are more widely spaced, *Figs. 21-23*, the crassulæ tend to be curved about the upper and lower margins of the oval primary pit-fields. "Forked," "split," or "fused" and very broad crassulæ, *Figs. 21* and *25*, are likewise of frequent occurrence.

Although the tracheary pitting of the redwood is commonly of the so-called opposite type, it readily passes over into typical alternating and closely crowded arrangements. When this change occurs, primary pit-fields and crassulæ are eliminated, *Figs. 27-29*, except in the case of such transitional or intermediate types of pitting as are illustrated in *Fig. 21*. In the redwood, as in *Cedrus* and other representatives of the Abietoideæ, the alternating orientation is of more frequent occurrence in roots than in stems; and, in the case of the aerial portions of the tree, in tracheids in close proximity to the primary wood and in the outer narrow rings of very old huge stems than in intervening tissue.

The individual bordered pits, which vary in diameter from 5-25 μ, may be circular, *Figs. 22, 23*, and *25*, oval or transversely elongated, *Fig. 30*, or flattened on one or more sides by close crowding, *Figs. 20, 21, 27*, and *29*. Many of them have conspicuously indented or notched contours, *Figs. 22, 23, 25*, and *26*. The pit apertures may be circular, oval, lenticular, or slitlike; their form and orientation fluctuating with variations in the physical structure (Zimmermann, 31) and thickness of the secondary walls of the tracheids.

When thin, transverse sections of normal tracheids are examined in polarized light with crossed nicols, the secondary walls are seen to con-

[1]In this paper, we have adopted the terminology proposed by the Committee on Nomenclature of the International Association of Wood Anatomists (6).

sist of three distinct layers, *Fig. 46*: (1) a thin, outer layer which transmits polarized light and is brilliant, (2) a thin, inner brilliant layer, and (3) an intervening layer of varying thickness which is dark or transmits less light than the inner and outer layers (Dippel, 7). The transmission of polarized light is closely correlated with the orientation of micellæ or chains of cellulose molecules. Where these are arranged parallel to the long axis of a tracheid, a layer appears dark in cross sections of the xylem; where they are oriented nearly at right angles, a layer is brilliant. The transmission varies at intervening angles. In other words, the micellæ of the thin inner and outer layers of the secondary wall tend to be oriented more nearly at right angles to the long axis of the cell, whereas those of the central layer are arranged either longitudinally or diagonally.

Variations in the thickness of the secondary wall are closely correlated with fluctuations in the width of the central layer, rather than of the inner and outer layers, *Fig. 46*. Where the central layer is relatively thin or inconspicuous, as, for example, in the large earlywood tracheids of old stems and roots, the pit apertures tend to be circular or transversely elongated; whereas in tracheids with thicker walls the apertures usually are lenticular or slitlike and are oriented either longitudinally or diagonally. The outlines of the apertures of a pit-pair may be superimposed or "crossed," the latter condition occurring where the orientation of lenticular or slitlike pits is diagonal. The secondary wall of the tracheids of "compression wood" differs from that of normal tracheids in having a wide inner layer, *Fig. 47*, which is coarsely and diagonally striated (Hartig, 16). This layer develops more or less numerous spirally arranged cracks during dehydration, and the apertures of the pits become extended far beyond the outlines of the borders.

The torus—i.e., the thicker central portion of the pit-membrane which stains intensely with Ruthenium Red or Haidenhain's Hæmatoxylin—varies markedly in size, form, and thickness. It may be absent, small and of irregular form, *Fig. 30*, or large, thick and disk-like, *Fig. 26*. Frequently it is conspicuously punctate, and the surrounding portion of the pit-membrane commonly tends to be more or less clearly striated or reticulated.

Bordered pits may develop in the tangential walls of the tracheids of both earlywood and latewood, particularly in the case of the narrower growth layers of old stems and roots. The tangential pits of the earlywood are larger, of sporadic distribution, and tend to have circular or oval apertures; whereas those of the latewood are smaller,

more numerous and uniformly distributed, and have lenticular or slit-like apertures. Crassulæ and primary pit-fields are absent in the tangential walls of the tracheids, but tori may be present in the bordered pits.

WOOD PARENCHYMA

The wood parenchyma of the redwood, as of many other Coniferæ, varies greatly in different parts of a single tree. It may be abundant and diffused throughout most of an annual ring, *Figs. 1, 7, 8,* and *11,* aggregated into more or less conspicuous zones, *Figs. 9* and *13,* confined to the latewood, *Fig. 2,* or much reduced in amount, *Figs. 4, 5, 6,* and *10.* Not infrequently it tends to be more abundantly developed in the inner than in the narrow outer rings of old stems and roots.

The individual strands of wood parenchyma fluctuate in length and in tangential diameter much as do the surrounding tracheary elements. This is due to the fact that both categories of cells are derived from the same fusiform initials, and therefore increase in size as the cambial initials become longer and wider. Minor differences in the length and cross-sectional area of parenchyma strands, as contrasted with tracheids, are due to differences in enlargement during tissue differentiation. The derivatives of the fusiform initials which divide transversely to form strands of wood parenchyma, do not elongate during differentiation of the xylem, whereas young tracheids may do so. The radial expansion of the parenchyma strands frequently tends to be less than that of the adjoining tracheids, but in the inner rings of roots the cross-sectional area of the parenchymatous elements may at times exceed that of the largest tracheids.

RAYS

Fisher (9), Essner (8), and Jaccard (18) have shown that rays vary in size and in number per unit area not only within different parts of a single tree but also within different parts of a single growth layer. In the redwood, as in the Coniferæ studied by Essner, the rays are smaller and more numerous, *Fig. 33,* in the innermost rings of stems and branches than in subsequently formed tissue, *Figs. 31, 32, 35-37.* This is due in part to an increase in height of the rays with concomitant ray-fusions, in part to an increase in the tangential diameter of the intervening tracheids, and in part to other factors. The height and width of the rays and the number of rays or ray cells per unit area are not constants, however, even in the outer growth layers of roots, branches, and stems, *Figs. 31, 32, 35-37.* The maximum height of the rays varies from a few cells to more than 75 cells, and the maximum

width from uniseriate to biseriate or triseriate and occasionally to multiseriate.

The individual ray cells fluctuate in size and form in different parts of a single tree and in homologous parts of different trees. The length, i.e., the radial dimension, of the ray cells varies from less than 35 μ to more than 500 μ; the depth, i.e., the vertical dimension, from less than 16 μ to more than 70 μ; and the width, i.e., the tangential dimension, from less than 9 μ to more than 40 μ. In general, the ray cells tend to be longer in earlywood than in latewood, in wide rings than in narrow ones, and in outer growth layers than in the innermost ones. Roots and the larger-celled growth layers of old stems tend to have broadly oval or "squarish" ray cells as seen in tangential sections, *Figs. 31, 36,* and *61;* whereas branches and the smaller-celled inner growth layers of stems commonly have narrower ray cells, *Figs. 32, 33, 35,* and *62,* in which the vertical dimension exceeds the tangential dimension. The ray cells, as seen in radial longitudinal sections of the xylem, may be uniformly rectangular or somewhat tapering in outline, with curved or diagonally oriented end walls. Furthermore, the marginal cells of the rays may be of approximately the same height as the central cells, or they may be much larger and provided with conspicuously curved outer walls.

PITS BETWEEN TRACHEIDS AND RAY CELLS

The ray cells of the redwood, as of the Taxodiaceæ, Araucariaceæ, Taxaceæ, Podocarpaceæ, Cupressaceæ, and Cephalotaxaceæ,[1] are provided with a more or less thickened primary wall, but do not form a true secondary wall such as is a characteristic feature of tracheary cells and of the rays of the Abietoideæ and most arborescent dicotyledons. This primary wall is derived directly from the ray initials of the cambium and is, in fact, a more or less modified cambial wall. As in the case of the ray initials, it is provided with more or less conspicuous primary pit-fields and plasmodesmata, i.e., sieve pitting, and tends to be conspicuously thickened at the angles of the cells where in contact with intercellular spaces, *Figs. 61,* and *62.* Simple pits and pits to intercellular spaces, which are characteristic features of the ray walls of the Abietoideæ, are entirely absent.

The presence of a true secondary wall in the rays of the Abietoideæ and its absence in the rays of the Taxodiaceæ, Cupressaceæ, etc., are of fundamental significance in any discussion of ray pitting. For

[1]Pilger's (25) nomenclature for the principal sub-groups of the Coniferæ is used throughout this paper.

example, there is at times a certain superficial resemblance between the end walls of the ray cells of *Juniperus* and those of *Cedrus*, *Abies*, or *Tsuga*. In *Juniperus* the investigator is concerned with deeply depressed primary pit-fields in primary walls, whereas in *Cedrus*, *Abies*, or *Tsuga* he is concerned with simple pits in secondary walls, i.e., entirely distinct morphological structures. In the case of pits in the "crossing field" or "tracheid field" of the rays of *Abies* or *Cedrus*, the investigator is dealing with half bordered pit-pairs; whereas in the rays of *Juniperus* or *Sequoia*, he is dealing with bordered pits which have no complementary simple pits on the ray side. The pit membranes are double structures formed by the wall of the ray and the adjacent primary wall of the tracheid, just as the tori and pit membranes of paired bordered pits are formed by the two adjacent primary walls of the tracheids.

The tracheary pits, which are visible through the crossing fields of the ray cells of the redwood, *Figs. 38-45*, vary in number from one to more than 20; in diameter, from less than 5 μ to more than 15 μ; in form, from circular or oval to asymmetrical; and in orientation from horizontal or vertical rows to diagonal or irregular groupings. The pit apertures, *Figs. 38-45*, may be slitlike, lenticular, or so much enlarged that the pit borders are more or less completely eliminated. Fusion of pit apertures, *Fig. 40*, or of both pit apertures and pit chambers, *Fig. 39*, are of not infrequent occurrence. Pit apertures may be oriented parallel to the long axis of the ray cells, *Fig. 38*, parallel to the long axis of the tracheids, *Fig. 45*, or in various diagonal positions, *Figs. 39-44*. As in the case of inter-tracheary pitting, variations in the orientation of the pit apertures are closely correlated with fluctuations in the thickness of the secondary wall of the tracheids and in the physical structure of its constituent layers.

The more conspicuous variations in the number and orientation of the pits within the outlines of a crossing field are correlated with fluctuations in the radial diameter of the tracheids and in the height of the ray cells. In other words, low ray cells in contact with narrow tracheids, *Figs. 39, 41*, and *43*, tend to have fewer pits per crossing field than similar ray cells in contact with wider tracheids, *Figs. 38, 40, 42*, and *45*, or than high ray cells in contact with either narrow or wide tracheids, *Fig. 44*. Where the crossing field is much elongated radially, the pits tend to occur in horizontal rows, *Fig. 38;* but where it is vertically elongated, the pits usually are oriented in vertical rows, *Fig. 44*. Thus, in the outer growth layers of old stems and roots, the orientation of the pits shifts from horizontal to vertical in passing from the wide tracheids of the earlywood to the narrow tracheids of the latewood.

SIEVE PITTING OF PARENCHYMATOUS CELLS

The wood parenchyma cells of the redwood resemble the ray cells in having a primary wall of varying thickness but no true secondary wall. Thus, in the case of both wood parenchyma and rays, the primary walls of adjoining parenchymatous elements are provided with more or less numerous plasmodesmata which may be evenly and uniformly distributed or aggregated in primary pit-fields. Where the plasmodesmata are numerous and evenly distributed, *Fig. 48,* as in the end walls of many ray cells and wood parenchyma cells, the walls are relatively smooth in sectional view, *Fig. 49.* On the contrary, where the plasmodesmata are aggregated in primary pit-fields, *Figs. 50, 51, 53, 54, 56, 57,* and *58,* the walls appear to be beaded or unevenly thickened in sectional view, *Figs. 52, 55,* and *59.* It should be emphasized in this connection, however, that where the walls are as tenuous as they are in the primary pit-fields (white areas) of *Figs. 54, 56, 57,* and *58,* it is difficult to demonstrate the delicate sieve structure in photomicrographs.

The primary pit-fields vary in size, form, depth, number, and distribution in the various surfaces of the parenchymatous elements and in different parts of the tree. As previously stated, there may be a single large sieve field, *Fig. 48,* in the end walls of the parenchymatous elements or a varying number of more or less discrete sieve areas which are located in primary pit-fields, i.e., thinner areas of the primary walls. The former condition tends to be of more frequent occurrence in thin-walled than in thick-walled cells, in the narrow outer rings of old stems and roots than in the inner growth layers, and in ray parenchyma than in wood parenchyma. The primary pit-fields usually are more widely spaced in side walls, *Figs. 58* and *59,* than in end walls, *Figs. 54-56;* in the side walls of much elongated ray cells than of shorter ones; and of earlywood than of latewood. Furthermore, where the ray cells are very broad, fewer primary pit-fields are visible in a single focal plane of a radial section than where the ray cells are narrower. It should be emphasized, in this connection, that the smoother appearance of the upper and lower ray walls in radial sections of the redwood, as contrasted with similar sections of the Abietoideæ, is due, in large part, to the absence of pits to the intercellular spaces.

TRAUMATIC RESIN CANALS

The cambium of the redwood is extremely sensitive to traumatic stimuli and to abnormal environmental influence and tends to form arcs of resin canals, *Figs. 8, 12, 14-19,* which extend considerable dis-

tances beyond the principal focus of stimulation. In other words, an injury to the crown may induce the formation of resin canals not only in the injured branches, but in the stem as well. The cambium of *Sequoia sempervirens* differs, however, from that of *Sequoia gigantea,* and particularly from that of the various species of *Cedrus,* in not forming horizontal resin canals.

The resin-canals of the redwood vary greatly in size and shape, in the character and abundance of the specialized cells which jacket them, in the presence or absence of tylosoids, and in the position of the canals within the growth layers, *Figs. 14-19.* The schizogenous cavities may be minute, *Fig. 15,* or relatively large, *Fig. 14.* They may be angular, *Fig. 15,* oval, circular, *Fig. 16,* slit-like, *Fig. 17,* or irregular, *Fig. 14.* They may have a conspicuous and clearly differentiated epithelium, *Figs. 16* and *19,* or irregular jacketing mixtures of strand tracheids and parenchyma, *Figs. 14, 17,* and *18.* The location of the resin canals is determined by the season of the year at which the abnormal stimulus occurs. Thus, the canals may be located in the first-formed portion of the earlywood, *Fig. 18,* in the outer portion of the latewood, *Figs. 14, 15,* and *17,* or in various intermediate positions, *Figs. 16* and *19.* They tend, in general, to be of more frequent occurrence in the branches and roots of old trees than in the clear length of the stem. It is significant, however, that in certain parts of the range of the redwood, the crowns of trees growing in exposed situations are injured each year by severe storms which occur at specific periods during the growing season. The stems of such trees frequently form arcs or rings of resin canals in a large proportion of the successively formed growth layers, *Fig. 12.*

STRAND TRACHEIDS

The redwood exhibits a strong tendency to form numerous strand tracheids not only in close proximity to traumatic resin canals, but also upon the outer surface of the latewood of growth layers or parts of growth layers which are devoid of resin canals, *Fig. 31.* Not infrequently they are developed with such regularity in successively formed growth layers as to appear of normal occurrence, but are in all probability due to some periodically recurring environmental stimulus.

RAY TRACHEIDS

Ray tracheids are of extremely uncertain and sporadic distribution in the redwood (Gordon, 13; Holden, 17). They may be abundantly developed in stems which exhibit no evidences of wounding and may be entirely absent in severely injured specimens. They may be aggre-

gated in a single independent radial row or erratically distributed along the margin of the rays. Their size and shape are variable, and their walls may be smooth or provided with helical thickenings.

CONTENTS OF PARENCHYMA AND "RESINOUS" TRACHEIDS

The ray cells and wood parenchyma strands of the redwood commonly contain a varying amount of ergastic material which varies in color from light yellow or orange to reddish-brown, dark red, or nearly black. It may be distributed in irregular masses, in large globules, or in finely granular or alveolar forms. In the heartwood of old roots, and of many stems and branches, not only do the walls of the tracheids become saturated with more or less of this material, but it exudes into the lumina, where it frequently forms septa, or plugs, which appear spool-shaped in sectional view, *Fig. 60*. Tracheids which contain such biconcave septa are commonly referred to as resinous tracheids (Penhallow, 24; Record, 26).

DISCUSSION

As stated in our introduction, systems of classifying and identifying the woods of conifers and dicotyledons have developed largely through trial and error. In other words, each investigator assembles, or has access to, a collection of relatively small samples of the wood of various genera and species. These specimens are sectioned and are laboriously and minutely studied in a search for structural differences which may be utilized in the construction of keys. Each investigator finds that certain of the diagnostic criteria used by his predecessors are unreliable and replaces them by others of putatively greater conservatism.

The inherent difficulty in this method of approaching the problem is that available collections of woods are extremely heterogeneous assemblages of fragmentary specimens from different sources. Samples of the wood of one species or genus may be from old virgin forest trees, those of another species or genus from young second-growth forests, and those of a third from trees planted in botanic gardens or arboreta. Therefore, the prevailing conception of the structural characteristics of the xylem of any particular species or genus depends upon chance, i.e., upon the types of specimens which happen to be available in existing collections. Students of commercial timbers naturally confine their attention to the merchantable part of the tree; but the parts of the tree which eventually reach the market vary with the species, with the uses to which different woods are put, and with many other factors.

In the case of *Sequoia sempervirens*, the properties of the wood and the commercial requirements are such that the outer parts of the clear lengths of old slowly growing trees are prized for industrial utilization. Therefore, it is not surprising that in such manuals as those of Koehler (20) and Brown (5) wood of the general type shown in *Fig. 4* is selected for study and illustration. It is significant, however, that the detailed anatomical descriptions of Penhallow (24) and of other botanists and paleobotanists appear to be based largely upon the investigation of similar material. The prevailing conception of the anatomical characteristics of *Sequoia gigantea* likewise is based upon the study of material from the outer portions of huge old stems, whereas that of other species and genera frequently is derived from an examination of specimens from young or immature stems.

Our detailed study of the redwood, and our preliminary observations upon the range of structural variability in various representatives of the Pinaceæ, Araucariaceæ, Taxaceæ, Podocarpaceæ, Taxodiaceæ, and Cupressaceæ, indicate that most, if not all, of the anatomical characters which have been utilized for diagnostic purposes fluctuate more or less, not only in trees grown under markedly different environmental conditions, but also within different parts of a single individual. This is as true of such supposedly conservative qualitative characters as form and orientation of pits, or of pit apertures, as of such quantitative characters as width of annual rings, dimensions of cells, or number of rays per unit area. In general, the range of variability tends to be greater in different parts of a single large mature tree than in homologous parts of different trees of the same species. There are significant anatomical differences not only in comparable parts of stems, roots, and branches, but also in growth layers formed at successive intervals during the development of each of these organs. Thus, although wood from the outer parts of huge old stems may resemble that of the root, it usually differs considerably from the wood of younger stems, of branches, or of seriously suppressed or dwarfed stems.

It is evident, in view of such facts as these, that, if the problem of classifying and identifying the woods of gymnosperms and angiosperms is to be attacked from a thoroughly scientific point of view, collections of authentic specimens must be assembled, not only from different genera, species, and varieties, but also from different parts of mature trees and from trees growing under different environmental conditions. The available anatomical data—tabulated from miscellaneous collections and without due regard to significant developmental, physiological, and ecological factors—do not provide a reliable basis for dis-

tinguishing the woods of most closely related species or even of many remotely related ones. This is particularly true of fossilized specimens which may be derived from any part of the tree and where such macroscopic aids as color, odor, gloss, hardness, etc., are evanescent. Thus, although it is possible to differentiate the wood of *Sequoia* from that of the Taxaceæ, Araucariaceæ, Abietoideæ, and Pinoideæ, and to determine, for example, that *Sequoia Penhallowii* is, in reality, a representative of the Abietoideæ, it is difficult to distinguish the wood of *Sequoia,* in all cases, from that of the Podocarpaceæ, Cupressaceæ, and other genera of the Taxodiaceæ. As indicated on preceding pages, the pitting of rays and of wood parenchyma—upon which Penhallow (24), Gothan (14), Kräusel (21), Kanehira (19), Slyper (30), and others place so much reliance—may fluctuate markedly within a single tree or species. For example, the pits in the crossing fields of the rays (earlywood) of the redwood vary from "taxodioid" to "cupressoid," "podocarpoid," or "glyptostroboid," depending upon the source of the wood that is selected for investigation. Similarly, the structure of the end walls of the wood parenchyma, as seen in tangential longitudinal sections of the xylem, may be smooth or conspicuously beaded (Taxodium type), depending upon the part of the tree from which the wood is cut.

In the seventh paper of this series, it was shown that such putative transitional Mesozoic Coniferæ as *Protopiceoxylon, Planoxylon, Thylloxylon,* and *Protocedroxylon* fall within the range of structural variability of living representatives of the Abietoideæ. These genera are characterized, as are *Cedrus, Keteleeria, Abies, Tsuga, Pseudolarix, Larix, Pseudotsuga,* and *Picea,* by ray cells which form true secondary walls. The question arises, accordingly, whether other representatives of the hypothetical transitional Araucariaceæ, which do not exhibit this type of ray structure, fall within the range of anatomical variability of the Podocarpaceæ, Taxodiaceæ, or Cupressaceæ.

The salient arguments for regarding *Brachyoxylon, Paracedroxylon, Telephragmoxylon, Anomaloxylon, Paraphyllocladoxylon,* and *Paracupressinoxylon* as araucarians in disguise rather than as representatives of the Podocarpaceæ, Taxodiaceæ, or Cupressaceæ are the reputed absence of crassulæ and the occurrence, particularly towards the ends of the tracheids, of so-called araucarian pitting. Emphasis is frequently placed, in addition, upon the occurrence of "resinous" tracheids and of clusters of medullary stone cells, and upon the absence of wood parenchyma and of clearly defined growth layers.

Clusters of sclerides or stone cells, *Fig. 34,* are of not infrequent occurrence in the pith of the redwood and have been reported in

Torreya, Podocarpus, Dacrydium, and *Cryptomeria* (Seward, 28). Typical "resinous" tracheids, *Fig. 60,* are abundantly developed in many specimens of *Sequoia sempervirens* and are known to occur in *Pinus* and other conifers exclusive of the Araucariaceæ. Wood parenchyma may be entirely absent in specimens of the wood of various representatives of the Taxodiaceæ and Podocarpaceæ and may be present in the secondary xylem of living representatives of the Araucariaceæ. Similarly growth layers may be strikingly differentiated in the Araucariaceæ and feebly developed or absent in the Podocarpaceæ, Taxodiaceæ, and Cupressaceæ. Furthermore, contiguity and alternation of tracheary pitting is by no means an infallible criterion of araucarian affinity. We have shown that in the redwood, as in *Cedrus* and other representatives of the Abietoideæ, the tracheary pitting shifts at times from an opposite to an alternating orientation and from a widely spaced to a closely crowded arrangement. Such changes in the arrangement of the bordered pits tend to occur most readily at the ends of the tracheary cells. It should be emphasized, in addition, that where the pits shift to the so-called araucarian orientation, crassulæ and primary pit-fields are more or less completely eliminated. An investigation of a wide range of Podocarpaceæ, Taxodiaceæ, and Cupressaceæ reveals not only that contiguity and alternation of tracheary pitting are of more frequent occurrence than has been hypothesized, but also that where the pits are in opposite or widely spaced arrangement, the crassulæ may be so tenuous that they can be demonstrated only after delicately controlled differential staining. Primary pit-fields and crassulæ which are clearly visible in sapwood may be completely obscured during the transformation of sapwood into heartwood. To assume that these delicate structures of the primary walls are preserved in visible form in all material and under all conditions of fossilization is illogical.

It is evident, accordingly, not only that there are no convincing arguments for assuming that the various Paracupressinoxyla and Brachyphylleæ are transitional or ancestral types of Araucariaceæ, but also that most of them fall within the potential ranges of variability of the Podocarpaceæ, Taxodiaceæ, or Cupressaceæ. A number of them, obviously, exhibit combinations of anatomical characters which occur in living representatives of the genus *Sequoia*. For example, *Telephragmoxylon* was instituted for woods of putative araucarian affinities which are characterized by having strand tracheids upon the outer surface of the latewood. We have shown that the redwood has a pronounced tendency to form strand tracheids and that, in trees from

certain parts of the range of the species, these strand tracheids are present upon the outer surface of many successive growth layers and thus appear to be of normal occurrence. Not only are typical schizogenous resin canals, "resinous" tracheids, and clusters of medullary stone cells of frequent occurrence in the redwood, but wood parenchyma may be greatly reduced in amount and practically eliminated from certain specimens. Thus, in so far as one may judge from published descriptions and illustrations, both species of *Telephragmoxylon* fall within the range of structural variability of *Sequoia,* and may, in fact, be remains of this genus or of some closely related one.

It should be emphasized in conclusion that, in the present status of our knowledge concerning the variability of diagnostic criteria and in view of the difficulty of accurately determining the generic and even the sub-family affinities of many specimens, specific names as applied to fossil woods have no significance other than as aids in designating particular specimens. The word, "species," must be used for the present in an entirely different sense from that in which it is employed in systematic botany. Many of the supposedly distinct "species" of fossil woods may actually have been derived from the same species or even from different parts of a single tree. Conversely, specimens which are referred to a particular "species" may actually have been derived from different species or genera. It should not be inferred from this, however, that the problem of identifying plants by the structure of their secondary xylem is necessarily a hopelessly difficult one. Not only is there the possibility of ultimately finding structures or characters which are present in one genus or species and entirely absent in others, but the ranges of structural variability vary in different plants. Thus, the *combinations* of structural characters that occur in specific parts of the tree may fluctuate from species to species.

SUMMARY AND CONCLUSIONS

1. A detailed investigation of the secondary xylem of the redwood demonstrates that most anatomical characters fluctuate considerably not only in trees grown under markedly different environmental conditions but also within different parts of a single tree. This is as true of such supposedly conservative qualitative characters as form and orientation of pits, or of pit apertures, as of such quantitative characters as width of annual rings, dimensions of cells, or number of rays per unit area.

2. In general, the range of variability tends to be greater in different parts of a single, large mature tree than in homologous parts of

different trees. There are significant differences not only in comparable parts of stems, roots, and branches, but also in growth layers formed at successive intervals during the development of each of these organs.

3. In the redwood, as in other conifers, the cambial initials and their derivatives increase in size for a varying period of years, after which they tend to remain constant except where deviations are induced by various modifying factors. The cells of roots and of the outer parts of the clear lengths of huge old stems tend to be larger than those of young stems, of physiologically dwarfed stems, or of branches.

4. Many of the salient variations in the size, form, number, and orientation of pits and of primary pit-fields are correlated with such fluctuations in the size of cells and in the thickness and physical structure of their walls. Thus, different combinations of anatomical characters tend to prevail in different parts of a tree and in tissues formed under varying growth conditions.

5. A preliminary study of the ranges of structural variability in various representatives of the Coniferæ indicates that although it is possible to differentiate the wood of *Sequoia* from that of the Taxaceæ, Araucariaceæ, Abietoideæ, and Pinoideæ, it is difficult to distinguish it in all cases from that of the Podocarpaceæ, Cupressaceæ, and other genera of the Taxodiaceæ.

6. Characters which have been interpreted as indications of araucarian affinities—i.e., contiguity and alternation of tracheary pitting, absence of crassulæ and of wood parenchyma, occurrence of "resinous" tracheids and of clusters of medullary stone cells, etc., are of not uncommon occurrence in the redwood and other representatives of the Podocarpaceæ, Taxodiaceæ, and Cupressaceæ.

7. There are no convincing arguments for assuming that the various Paracupressinoxyla and Brachyphylleæ are transitional or ancestral types of Araucariaceæ, rather than forms related to the Podocarpaceæ, Taxodiaceæ, or Cupressaceæ. A number of them exhibit combinations of anatomical characters which fall within the potential range of structural variability of the genus *Sequoia*.

8. Systems of classifying and identifying the woods of gymnosperms and angiosperms have developed largely through trial and error. Available anatomical data—tabulated from miscellaneous collections of more or less fragmentary specimens and without due regard to significant developmental, physiological, and ecological factors—do not provide a reliable basis for distinguishing the woods of most closely related species and of many remotely related ones.

9. If the problem of classifying and identifying the woods of gymnosperms and angiosperms is to be attacked from a thoroughly scientific point of view, collections of authentic specimens must be assembled, not only from different genera, species, and varieties, but also from different parts of mature trees and from trees growing under different environmental conditions.

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DESCRIPTION OF PLATES

PLATE 99

Sequoia sempervirens

Figs. 1-5. *Stem.* Transverse sections of the xylem, showing structural details of growth layers at successive intervals between the pith and bark of a large stem. × 32.

PLATE 100

Sequoia sempervirens

Fig. 6. *Stem.* Transverse section of the xylem from the outermost portion of an old tree, showing wide layer of "compression wood." × 32.

Figs. 7 & 8. *Branch.* Transverse sections of the xylem, showing growth layers from the inner and outer parts of an old branch. × 32.

Fig. 9. *Branch.* Transverse section of the xylem from the under side of an old branch, showing "compression wood." × 32.

Fig. 10. *Root.* Transverse section of the xylem of an old root. × 32.

PLATE 101

Sequoia sempervirens

Fig. 11. *Stem.* Transverse section of the xylem of a young vigorous tree, showing wide growth layer and gradual transition between earlywood and latewood. × 17.

Fig. 12. *Stem.* Transverse section of the xylem, showing traumatic resin canals in the latewood of three successive growth layers. × 17.

Fig. 13. *Stem.* Transverse section of the xylem, showing wide growth layer formed after a prolonged period of suppression. × 17.

PLATE 102

Sequoia sempervirens

Figs. 14, 17-19. *Stem.* Transverse sections of the xylem, showing various types of traumatic resin canals. × 54.

Fig. 15. *Root.* Transverse section of the xylem of a young root, showing traumatic resin canals. × 54.

Fig. 16. *Root.* Transverse section of the xylem of an old root, showing traumatic resin canals. × 54.

PLATE 103

Sequoia sempervirens

Figs. 20-25. *Stem.* Radial longitudinal sections of the xylem, showing variations in the form and in the distribution of primary pit-fields, crassulæ, and bordered pits in thin-walled tracheids of varying diameters. × 255.

Figs. 27-29. *Root.* Radial longitudinal sections of the xylem, showing compressed and alternating arrangements of bordered pits. × 255.

Figs. 26 & 30. *Stem.* Radial longitudinal sections of the xylem, showing variations in the size and form of the torus. × 1680.

PLATE 104

Sequoia sempervirens

Fig. 31. *Stem.* Tangential longitudinal section of the xylem, showing strand tracheids, rays, and bordered pits. × 54.

Fig. 34. *Stem.* Transverse section of the pith, showing cluster of stone cells. × 73.

Figs. 32, 33, 35-37. *Stem.* Tangential longitudinal sections of the xylem, showing common variations in the size and form of rays and of their constituent cells. × 54.

PLATE 105

Sequoia sempervirens

Figs. 38-43, & 45. *Stem.* Radial longitudinal sections of the *first formed part* of the earlywood of various growth layers, showing variations in the size, form, number, and orientation of bordered pits in the "crossing fields" of the rays. × 1210.

Fig. 44. *Root.* Radial longitudinal section of the xylem of a young root, showing orientation of bordered pits in the crossing field of a ray. × 1210.

Fig. 46. *Stem.* Transverse section of the xylem, photographed with polarized light. × 965.

Fig. 47. *Stem.* Transverse section of "compression wood," photographed with polarized light. × 965.

PLATE 106

Sequoia sempervirens

Figs. 48 & 51. Tangential longitudinal sections of the xylem, showing surface views of the sieve pitting in the end walls of ray cells. × 500.

Figs. 50, 53, 54, 56, & 57. Transverse sections of the xylem, showing primary pit-fields and sieve pitting in the end walls of wood parenchyma. × 500.

Figs. 49, 52, 55. Tangential longitudinal sections of the xylem, showing sectional views of the end walls of wood parenchyma. × 500.

Fig. 58. Transverse section of the xylem, showing surface view of the wall of a ray cell. × 500.

Fig. 59. Tangential longitudinal section of the xylem, showing sectional view of the lateral walls of wood parenchyma. × 500.

Fig. 60. Radial longitudinal section of the xylem, showing "resinous tracheids." × 170.

Figs. 61-62. Tangential longitudinal sections of the xylem, showing details of ray structure. × 500.

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